Inter-tidal Ecology at Narrow Neck Reef, New Zealand (Studies in Inter-tidal Zonation 3.)[1]

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INTRODUCTION

THE PLANT and attached animal communities at Narrow Neck Reef, Auckland, have been studied in relation to factors that may be concerned with determining their vertical zonation. Observations were made between January, 1947, and July, 1948.

Certain levels on the shore appear to be more critical than others in determining the upper and lower limits of species and of communities; these levels may coincide with heights above low water at which there is a sudden change in environmental conditions. In accordance with the general aim of this series, an investigation has been made into the number and position of levels which may be critical at Narrow Neck.

Acknowledgments: The writer wishes to express her sincere appreciation to Professor V. J. Chapman for assistance and helpful criticism throughout this work; to Dr. G. F. Papenfuss and to Miss L. B. Moore for advice on the text; to Mr. V. W. Lindauer for assisting with the identification of Phaeophyceae and Rhodophyceae; to Mr. J. E. Morton for identification of the animals; and to Mr. L. Finch for help with the compilation of the map.

TERMINOLOGY

While it is not proposed to enter into a lengthy discussion on the controversial topic of marine ecological terminology, it does appear essential to state precisely the sense in which each term is employed. However, it seems unreasonable to me either to give new meanings to words now in current use in ecological nomenclature, or to impose a new series of technical terms on an already overburdened vocabulary.

As the word "littoral" has been used in so many different ways, I prefer to call that part of the shore between extreme high water mark of spring tides and extreme low water mark of spring tides the "inter-tidal region," where these extreme levels are the means of monthly extremes for the locality over a number of years. The area between Mean Extreme Low Water Spring Tide and Extraordinary Low Water Spring Tide (= Auckland Harbour Board Datum) corresponds to Stephenson's sublittoral fringe. Below this is the sublittoral or subtidal region, which is never exposed by the tide. That part of the shore from above Extreme High Water Spring Tide to the upper limit of wind-borne spray is regarded as the supralittoral, or supratidal region. It includes the somewhat arbitrary "splash" and "spray" zones, neither of which is of much importance at Narrow Neck.

Within the inter-tidal region exists a number of marine biotic communities. Some authors consider that these should be treated as though they were equivalent to terrestrial climax communities. In general, however, the marine units occupy smaller areas and may be much less long-lived, owing to the shorter life-history of the component organisms and to the super-position of the tidal factor on the climatic complex. On the other hand, because of this relative impermanence

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as compared with, for example, forest vegetation, it could be maintained that the units do not justify the ecological status of a climax. In this paper, support is given to the former view; for there does appear to be a certain, fairly constant sequence of events which may be in the nature of a true succession leading up to a relatively stable climax condition. Nevertheless, more detailed work will be necessary for a satisfactory elucidation of this problem.

In assessing the ecological importance of animals in a community, one of three views may be adopted: (1) that animals are biotic factors external to the plant community; (2) that animal communities exist where plants form part of the habitat; (3) that plants and animals are interrelated, co-acting constituents of an integrated biotic community (Phillips, 1931). The third view is adopted by several authors, including Clements and Shelford (1939), who propose the biome or biotic formation as the basic unit on land or sea. The concept seems the most suitable one so far put forward for application to seashore communities and is adopted in the present work.

The broad vertical zonation in the Hauraki Gulf can be compared with that described by Stephenson (1939; 1944) for the coast of South Africa, and more recently by Dakin, Bennett, and Pope (1948) for the New South Wales coast. Four main zones can be distinguished here, of which characteristic dominants are: (1) *Melaraphe* (a littorinoid species), (2) barnacles, (3) small, turf-forming algae, and (4) large, brown algae. Each zone is regarded as constituting a separate biome, or biotic formation, since these divisions appear to be real entities of world-wide occurrence. Using Stephenson's terminology, these are equivalent to: (1) littorina zone, (2) balanoid zone, (3) mixed algal zone, and (4) sublittoral fringe.

In this paper, terms used in connection with the ecology of higher plants have been applied to units on the seashore, according to the following definitions:

Biome: a biotic community with the rank of a climax formation (Clements and Shelford, 1939).

Association-complex: a group of associations occurring in successive belts which follow one another in a regular, constantly recurring sequence (Cranwell and Moore, 1938).

Association: a climax community with two or more dominants (Clements, 1916).

Consociation: a climax community with a single dominant (Phillips, 1931).

Fasciation: a portion of an association in which one or more dominants have dropped out and have been replaced by other forms, the general aspect of the community remaining unchanged (Clements, 1936).

Clan: a small community of subordinate importance but of distinctive character, frequently the result of vegetative propagation (Clements, 1936).

Aspect society: A seasonal community characterized by one or more subdominants.

Belt: a continuous, horizontal strip of the coast occupied throughout most of its length by one association, which may be interrupted by another community, depending on slightly local conditions (Cranwell and Moore, 1938).

Zone: the horizontal sector occupied by one formation and characterized by dominants of one or more associations.

PHYSICAL FACTORS

Narrow Neck lies about 2 miles north of Devonport, on the north shore of Waitemata Harbour, Auckland. The Harbour constitutes a ramifying arm of the Hauraki Gulf, which is almost landlocked and protected from the full force of onshore gales from the Pacific Ocean by Great Barrier and Little Barrier Islands to the north and by Coromandel Peninsula to the east. The reef itself forms part of a submarine shelf extending seawards to the Rangitoto Channel, the greatest depth of

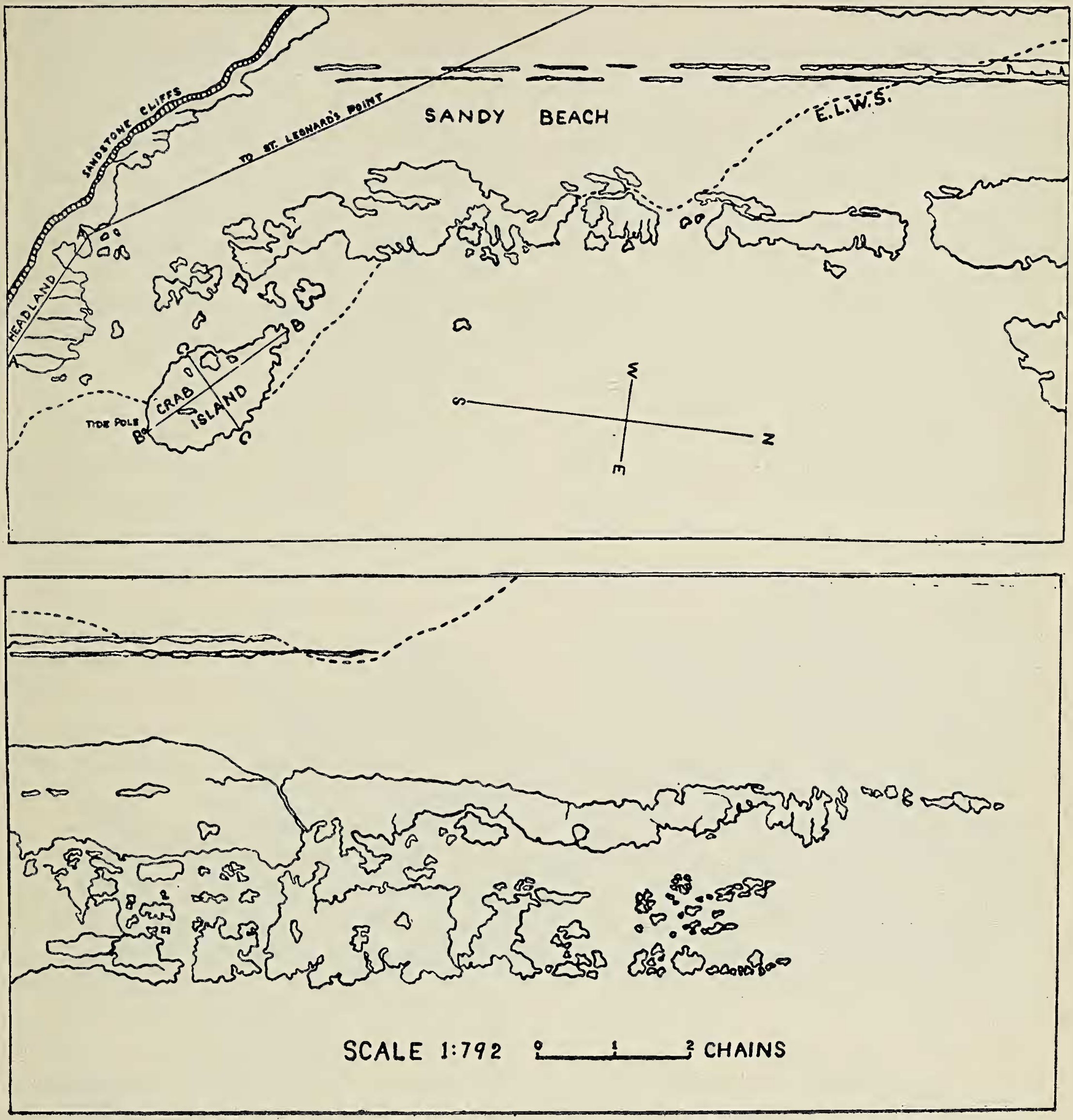

FIG. 1. Map of Narrow Neck Reef, showing position of Traverses A, B, and C. Traverse A, on Headland, top left; Traverses B and C, on Crab Island.

water at any point surrounding the reef being 2.5 fathoms. A thin layer of fine silt and mud is deposited on the gently inclined, exposed rock surface in calm weather.

There are two drainage outlets in the vicinity: one at the southern end of Narrow Neck Beach, the other at St. Leonard's Point. A considerable increase in both turbidity of water and abundance of colonial diatoms is apparent about these places. The area studied most intensively extends from the northern end of Narrow Neck Beach to St. Leonard's Point, a distance of about five-eighths of a mile.

The reef is made up of three main groups of rock which have been named the Headland, Crab Island, and the Main Reef (see map, Fig. 1). The Headland at the cliff base is barely covered by an extreme high spring tide. Crab Island (so-called because of the abundance of the large shore crab, *Leptograpsus variegatus*) is a small island of rock which, although slightly more elevated than the Main Reef, is covered by even the lowest high tides. At no point is the Main Reef higher than M.S.L. (6.22 feet above Auckland Harbour Board Datum).

The rock is a heterogeneous, fine, volcanic agglomerate, locally known as Parnell Grit (Bartrum and Turner, 1928). This is conformably interbedded with Waitemata Sandstone, which forms the major part of the Auckland Isthmus. There are a large number of irregular joints in the rock, along which deposition of brittle iron compounds has taken place.

The Auckland district has a maritime climate, with a relatively small daily and annual variation in temperature and precipitation (Beveridge and Chapman, 1950). Prevailing westerly winds are off-shore at Narrow Neck, and hence wave action is usually slight. Sea temperature closely follows that of the surrounding land.

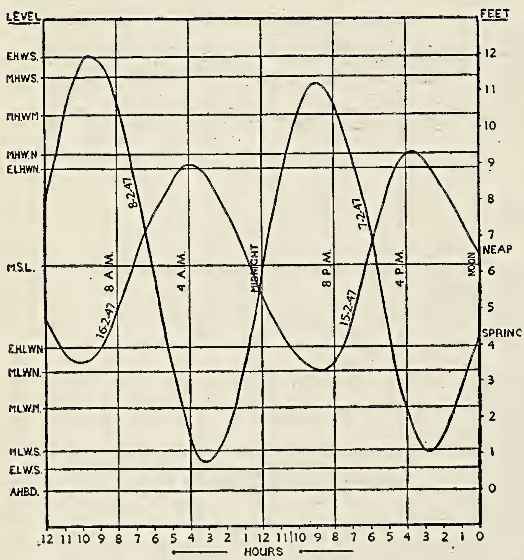

FIG. 2. Chart indicating extreme tidal ranges recorded over two 24-hour periods in the month of February, 1947, by the self-registering tide gauge at Queen's Wharf, Auckland.

There are no fresh-water outlets which would have a significant effect on the salinity of seawater in the locality. Isolated determinations were made by Hounsell (1935) at North Head, 2 miles south of Narrow Neck, and at Rangitoto Beacon to the east, where the values were 35.00 and 35.10, respectively. Both samples were collected in the morning.

The *p*H of seawater at Narrow Neck lies between 8.0 and 8.1, the value remaining constant throughout the year (Ambler and Chapman, in press).

Tides in the Hauraki Gulf are semidiurnal, with an extreme spring range of about 12 feet and an extreme neap range of about 5 feet. Day and night tides differ slightly in amplitude, the night tides being greater in summer and smaller in winter. Figure 2 shows typical extreme neap and spring tides recorded for the locality by the Auckland Harbour Board. It was found from readings on a tide pole at Narrow Neck that there is no significant disparity in time and rate of tidal rise and fall in comparison with the recordings on the self-registering tide gauge at Queen's Wharf.

Tide levels were averaged from Auckland Harbour Board marigrams for the years 1945, 1946, and 1947 in order to avoid using data for 1 year only. The method of calculating the levels was that used by Beveridge (in Beveridge and Chapman, 1950). There is no significant difference between the figures for 3 years presented in Table 1 and those of Beveridge and Chapman for the year 1945. Extreme figures in Table 1 are means of monthly extremes. All heights are expressed in feet above Auckland Harbour Board Datum (0.00 feet, or Extraordinary Low Water Spring Tide).

TABLE 1
TIDAL DATA FOR AUCKLAND HARBOUR

TIDE LEVEL	HEIGHT IN FEET ABOVE A.H.B.D.
Extreme High Water Springs (E.H.W.S.)	11.95

Mean High Water Springs (M.H.W.S.)	11.41
Mean High Water Mark (M.H.W.M.)	10.35
Mean High Water Neaps (M.H.W.N.)	9.28
Extreme (Lowest) High Water Neaps (E.(L).H.W.N.)	8.88
Mean Sea Level (M.S.L.)	6.22
Extreme (Highest) Low Water Neaps (E.(H).L.W.N.)	3.96
Mean Low Water Neaps (M.L.W.N.)	3.29
Mean Low Water Mark (M.L.W.M.)	2.29
Mean Low Water Springs (M.L.W.S.)	1.12
Extreme Low Water Springs (E.L.W.S.)	0.60
Auckland Harbour Board Datum (A.H.B.D.)	0.00

LEVELING SURVEY

To obtain quantitative data concerning the levels and vertical range of the more important littoral plants and animals, a series of traverses was made in different parts of the area (see Figs. 1 and 3–6). In each case, the leveling staff was placed as near as possible to the average limit of the vertical range of the species. Elevation or depression levels due to local modifications were not taken into account. Levels of species such as *Caulerpa sedoides* and *Splachnidium rugosum* which did not occur across the paths of the traverses were obtained as isolated spot-heights from elsewhere within the area. The traverses were

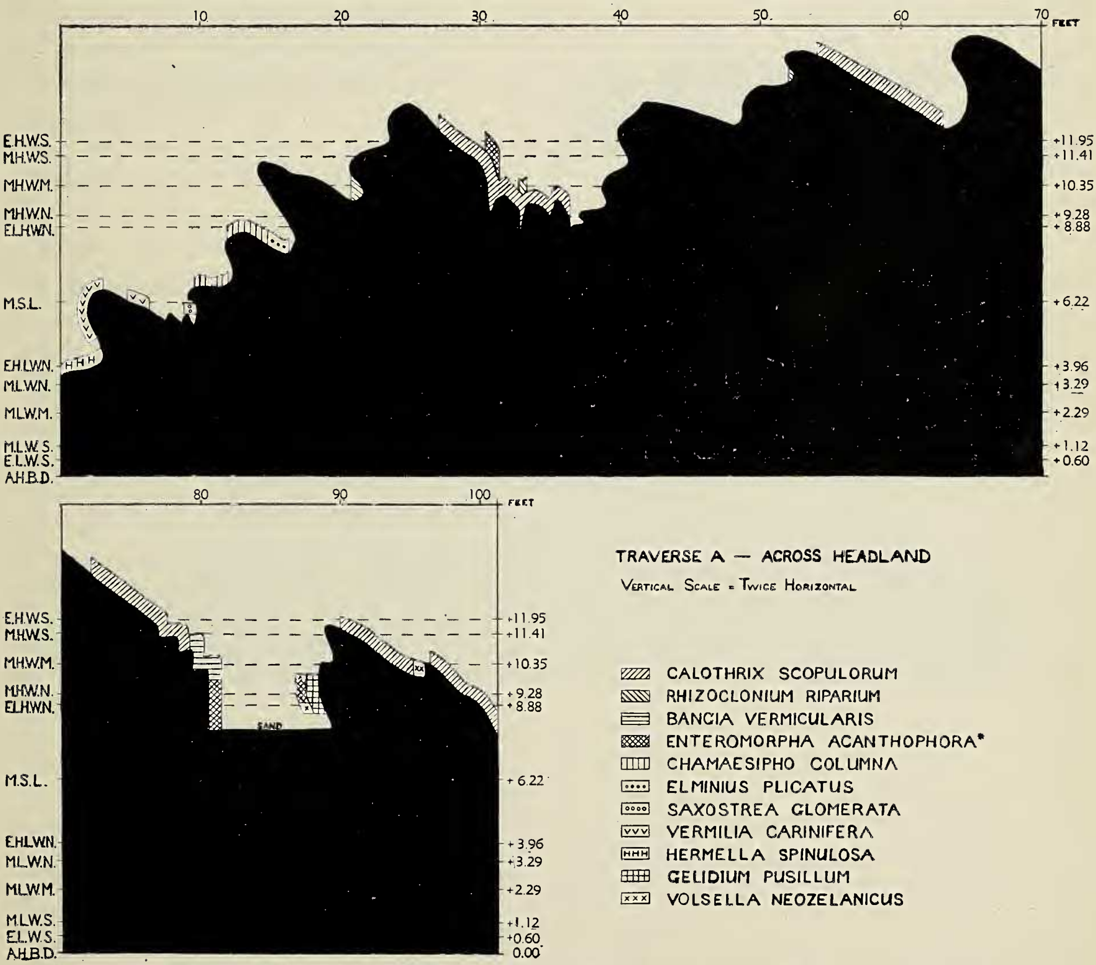

FIG. 3. Traverse A. (* Found to be *Enteromorpha procera* f. *minuta*.)

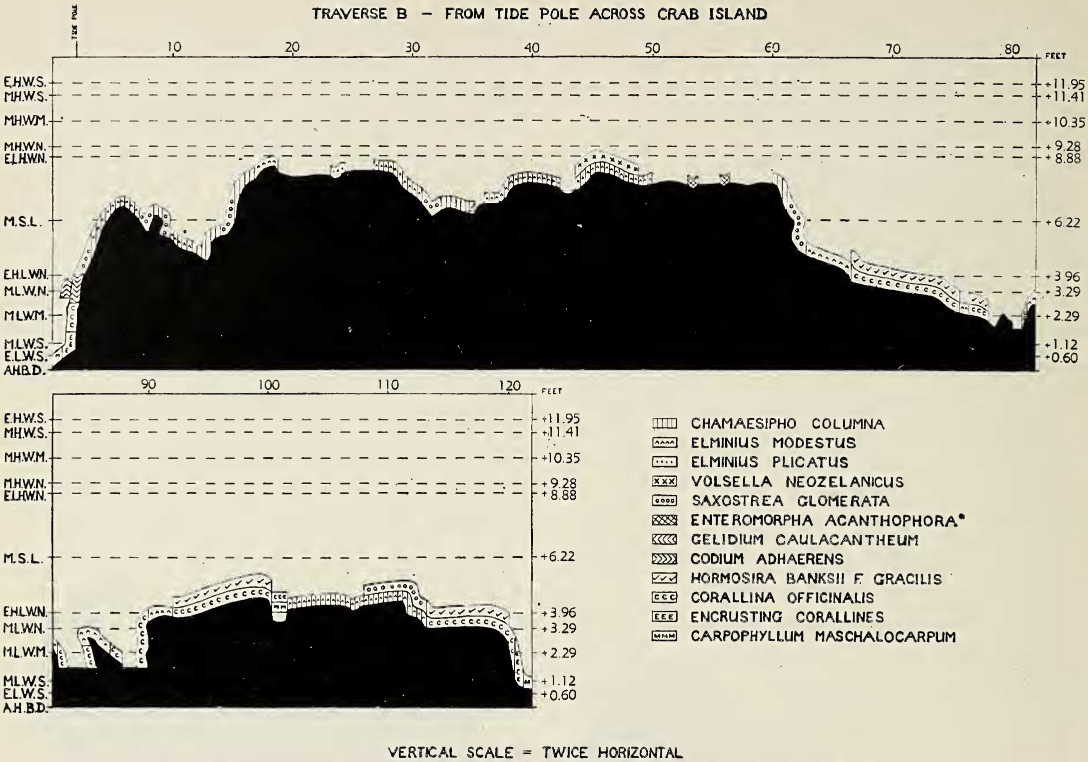

FIG. 4. Traverse B. (* Found to be *Enteromorpha procera* f. *minuta*.)

mapped in late summer (January–February, 1948) and therefore include summer aspect societies.

Traverse A (Figs. 1, 3): Across Headland; length 101 feet; bearing 116° 20′.

This traverse was designed to illustrate typical zonation of the communities at higher levels. It passes from M.L.W.N.[3] to above E.H.W.S. and crosses in front of a small cave. The angle of dip of the rock, which is to the north, is clearly indicated. Dip faces of the inclined ledges are exposed to maximum insolation, while strike faces are shaded for most of the day. The different aspects show differences in the species colonizing the same level: for instance, near the end of the traverse, *Gelidium pusillum* and *Volsella neozelanicus* flourish on a shaded, vertical strike face at the same level as *Calothrix scopulorum,* which usually grows above them.

In front of the cave mouth (between 80 and 90 feet) the sand level limits the downward colonization of *Enteromorpha procera* f. *minuta.*

Traverse B (Figs. 1, 4): Crab Island, from the tide pole across the longer axis of the island; length 122 feet; bearing 136° 30′.

In Traverse B the relative positions above A.H.B. Datum of the more important communities below E.(L).H.W.N. can be seen. The traverse starts at A.H.B.D., at which level *Carpophyllum maschalocarpum* is flourishing, and passes upwards successively through encrusting corallines, *Corallina officinalis, Gelidium caulacantheum,* oysters, and barnacles. It illustrates the wide extent of both the balanoid community at higher levels and of *Corallina* and *Hormosira* lower down on flat surfaces. The steeply ascending rock slope at the beginning of the traverse is shaded for

[3]See Table 1 for full explanation of abbreviations used throughout this paper.

most of the day and has a southwesterly aspect. *Codium adhaerens* flourishes here while *Hormosira* is absent. Telescoping of belts with increasing angle of slope is evident.

Traverse C (Figs. 1, 5): Crab Island, across the shorter axis, at right angles to Traverse B; length 70 feet; bearing 46° 40′.

Traverse C shows Crab Island in profile from the shore to the seaward face of the island. The change in nature and in specific composition of communities with change in level is very similar to that in Traverse B. *Enteromorpha procera* f. *minuta* and *Elminius plicatus* are poorly developed on Crab Island. It will be observed that the encrusting coralline belt descends lower than usual to seaward. *Corallina* and *Hormosira* are growing just below the 8-foot level, 4 feet above their normal upper limit, under pool conditions.

Traverse D (Figs. 6*a, b*): St. Leonard's Point; length 269 feet; bearing 45°.

Traverse D, the longest, runs in a direct line from high to low water. It is not shown on the map of the reef because the shape of the area as a whole is too awkward to allow the inclusion of St. Leonard's Point on a map of that scale.

The strata of the cliffs above the point are not tilted as they are at the Headland. The dip and strike of the ledges below form a correspondingly regular sequence from the cliff base to the seaward end of the point. Much of the intervening rock is flat and is covered with thick deposits of mud. The water about the point is always turbid with much suspended matter from the sewage outflow. The general zonation, however, is remarkably similar to that obtaining at Narrow Neck.

Melaraphe oliveri and *Calothrix scopulorum* are widespread between M.H.W.S. and E.H.W.S. Beneath the overhanging ledge 36 feet from the start of the traverse, *Ralf-*

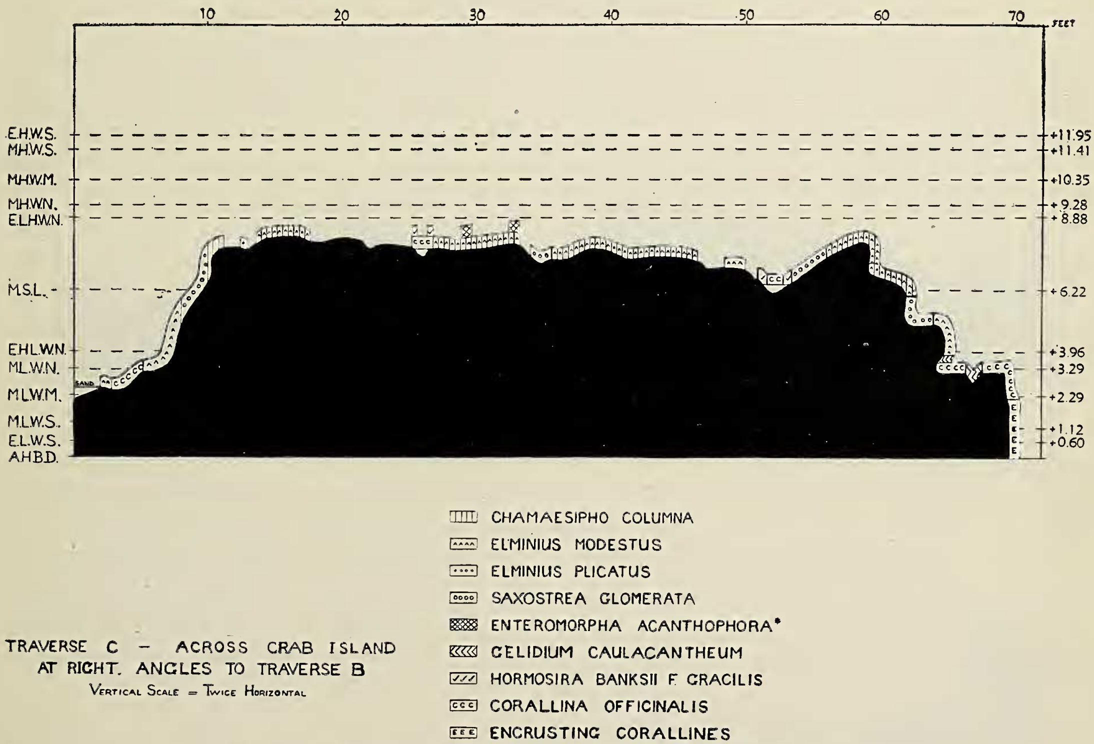

FIG. 5. Traverse C. (* Found to be *Enteromorpha procera* f. *minuta*.)

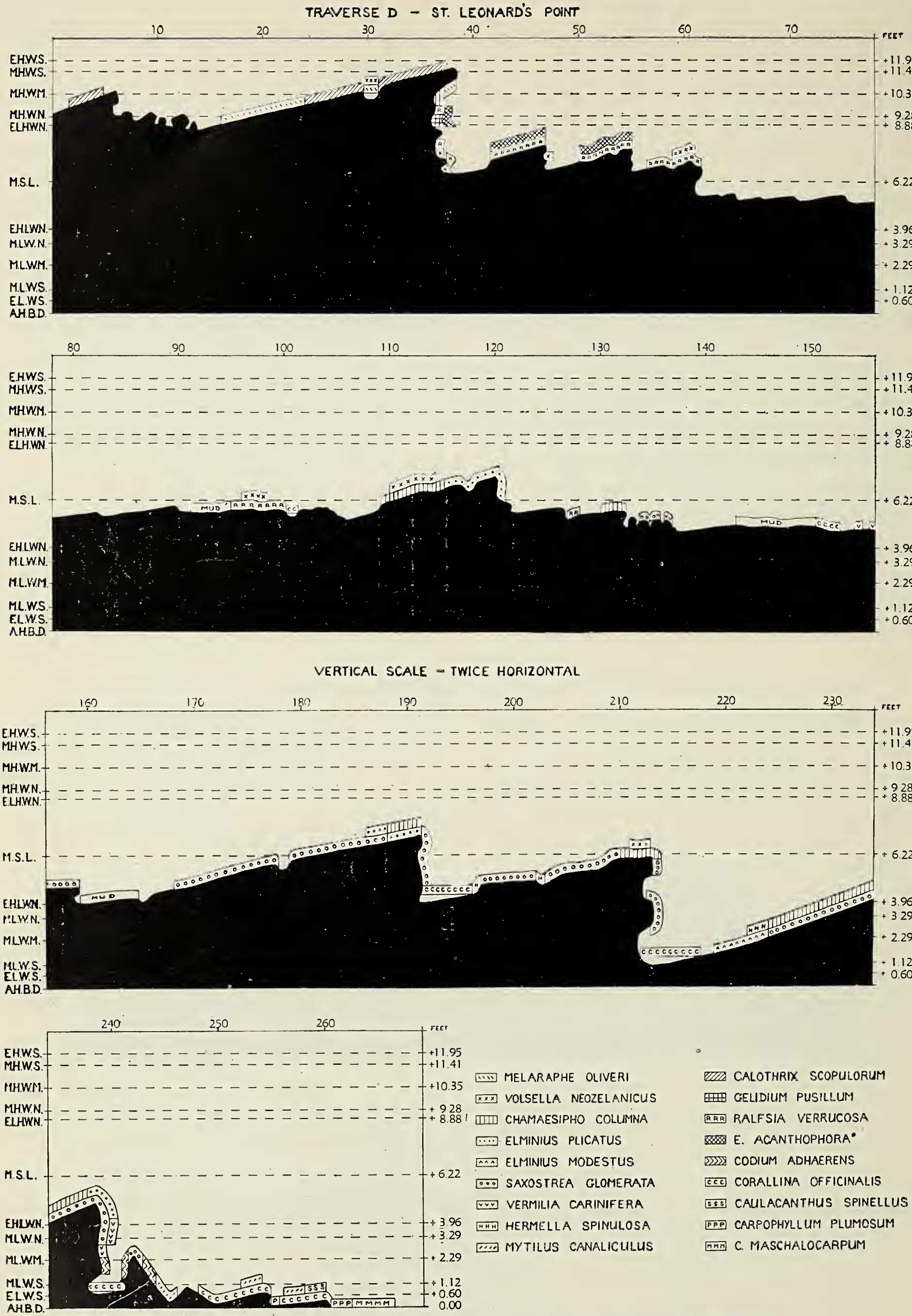

FIG. 6. Traverse D. (* Found to be *Enteromorpha procera* f. *minuta.*)

sia verrucosa and *Enteromorpha procera* f. *minuta* are growing above their normal level. Together with *Volsella neozelanicus* they colonize wide stretches of the relatively flat rock about M.S.L. Slight elevations are marked by a local increase in abundance of the large barnacle *Elminius plicatus.* The chief difference between St. Leonard's Point and Narrow Neck Reef lies in the presence of the *Mytilus*—Attached Algae Community at the former locality about E.L.W.S. (see p. 370).

From data obtained in the leveling survey, Figure 7 was constructed by plotting the vertical ranges of 25 of the more important plants and animals against the curve for the percentage of annual exposure at each level. The average amount of exposure and submergence endured by each species can therefore be calculated from this chart. (Each limit represents the average of several readings on the leveling staff.)

BIOTIC COMMUNITIES

These are described roughly in their order of occurrence from high to low water. It should be observed, however, that the upper limit of one association may overlap the lower limit of the one immediately above: for example, the lower limit of the *Corallina*—*Hormosira* association is given as 0.8 feet, while the upper limit of the Encrusting Coralline association is 1.7 feet. This may be explained by local differences in such factors as topography and exposure to wave action which tend to allow the replacement of one community by another. Thus, a horizontal as well as a vertical sequence with changed conditions of habitat may be distinguished. The range of exposure undergone by each community is expressed as a percentage of the total possible exposure per annum.

Littorina Formation

1. Calothrix—Melaraphe Association

Vertical range: 12.9–9.2 feet. Between E.H.W.S. and M.H.W.N.

Exposure: 100–78 per cent.

Calothrix scopulorum (d)[4]
Rhizoclonium riparium (ld)
Enteromorpha procera f. *minuta* (f)
Microcoleus acutissimus (o)
Melaraphe oliveri (d)
Lyngbya lutea (a)
Lophosiphonia macra (lf)
Monostroma latissimum (r)

Two separate consociations are recognizable:

a. Calothrix Consociation

The dull, blackish-green crusts of *Calothrix scopulorum* cover extensive areas of exposed rock about the highest levels of the intertidal region, especially on flat or gently sloping surfaces exposed to strong insolation. After a high spring tide or a heavy rain, the thick sheaths surrounding the trichomes become extremely gelatinous. *Calothrix* does not tolerate stagnation because in small, water-filled depressions, in which *Lophosiphonia macra* is often present, growth of *Calothrix* ceases abruptly. During periods of continuous exposure, the encrusting mat becomes dry and cracked and peels off easily. At such times the rock colonized by *Calothrix* may become white because of salt efflorescence. The upper limit of the consociation, which is much more clearly defined than the lower, is probably correlated with sudden extreme changes in salinity and microclimate. An example of sudden temperature changes in the *Calothrix* belt was recorded on February 8, 1948. At noon, rock temperature reached 33.3° C. After a brief shower it fell to 24° C.

b. Melaraphe Consociation

As *Calothrix* becomes sparser in the lower 2 feet of its vertical range, the small gastropod *Melaraphe oliveri* assumes dominance.

[4] d = dominant, o = occasional, a = abundant, l = local, f = frequent, r = rare

The boundaries of this community cannot be delimited precisely in terms of tide levels since *Melaraphe* is able to move within a relatively restricted area to a more favorable

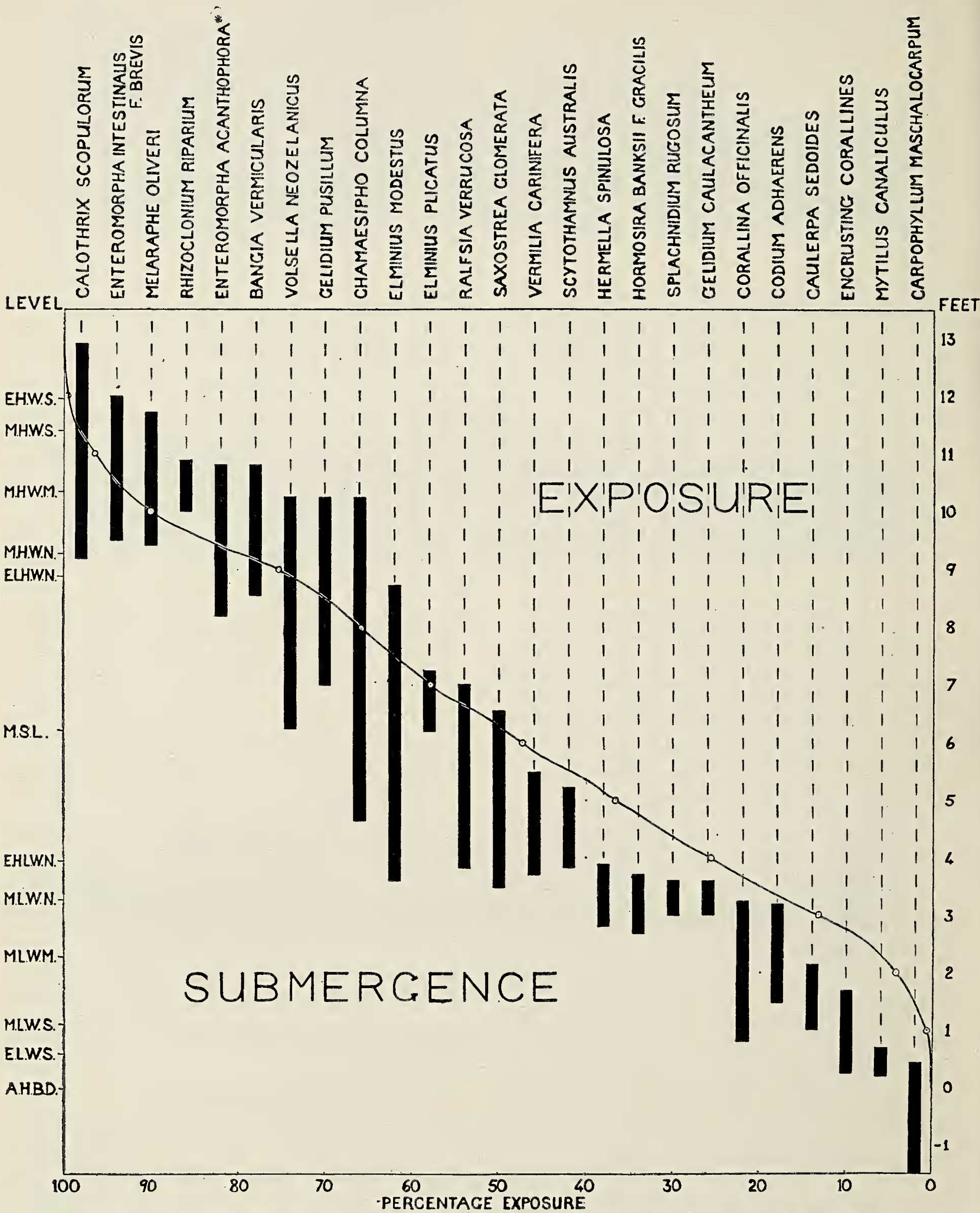

FIG. 7. The vertical range of 25 inter-tidal species (* found to be *Enteromorpha procera* f. *minuta*) in relation to annual percentage exposure and submergence. (The limits are averaged from data obtained in the four traverses.)

local environment. During a hot summer afternoon, when the tide is low, it will migrate to a shallow pool beneath an overhanging ledge, while just after being uncovered by the tide it will present a more uniformly scattered pattern of distribution.

Balanoid Formation

2. **Enteromorpha — Gelidium — Volsella (Modiolus) Association**

Vertical range: 10.8–6.3 feet. Between M.H.W.M. and M.S.L.

Exposure: 94.7–58 per cent.

Enteromorpha procera f. *minuta* (d)
Volsella (Modiolus) neozelanicus (d)
Chamaesipho columna (a)
Onchidella patelloides (o)
Gelidium pusillum (d)
Ralfsia verrucosa (a)
Centroceras clavulatum (f)
Elminius modestus (f)

Although sometimes epiphytic on *Gelidium pusillum, Enteromorpha procera* f. *minuta* more often dominates in exposed situations immediately below the *Calothrix—Melaraphe* association. The small mussel *Volsella (Modiolus) neozelanicus* is usually entangled within the dense cushions formed by *G. pusillum.* Striking evidence of the reactions of these species to exposure and shelter is seen on the rock face south of the Headland cave (Traverse A, Fig. 3). Where the slope is vertical, with a curve that faces the incoming tide, *Enteromorpha* dominates. Where the rock is shaded or overhanging, the dominants are *Volsella* and *Gelidium.*

a. **Enteromorpha Consociation**

E. procera f. *minuta* fluctuates seasonally in abundance. Although present all the year round, it reaches maximum extent in autumn and winter, with a secondary growth period in spring. During the hottest summer months (January and February) the *Enteromorpha* community on wharf piles in the Auckland

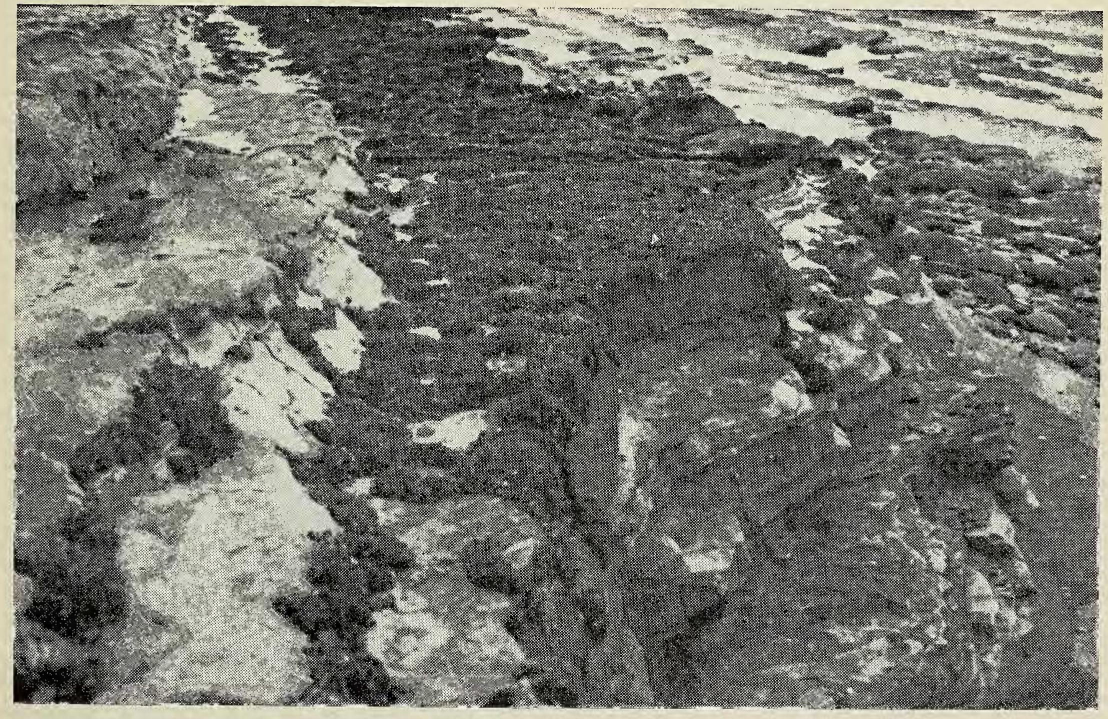

FIG. 8. *Volsella neozelanicus* consociation on a flat ledge between Narrow Neck and St. Leonard's Point.

Harbour is absent, though still growing at similar levels in the Narrow Neck locality. The mat formed by this species serves as a trap for sand and silt, which act as a moisture reservoir during periods of exposure by the tide.

b. **Volsella Consociation** (Fig. 8)

Volsella neozelanicus may be profoundly dominant below the level usually colonized by *Gelidium*. This suggests that the upper limit of *Volsella* is raised through association with the red alga, the thallus of which acts like a sponge in conserving moisture.

The barnacles *Chamaesipho columna* and *Elminius modestus* and the encrusting *Ralfsia verrucosa* are subordinate members of this community.

3. **Chamaesipho — Elminius — Saxostrea Association** (Fig. 11)

Vertical range: 10.2–3.6 feet. Between M.H.W.M. and M.L.W.N.

Exposure: 92–21.3 per cent.

Chamaesipho columna (d)
Saxostrea glomerata (d)
Scytothamnus australis (ld)
Enteromorpha procera f. *minuta* (a)
Splachnidium rugosum (f) (summer)
Pylaiella novae-zelandiae (f)
Caulacanthus spinellus (o)
Gelidium caulacantheum (o)
Bangia vermicularis (o) (winter)
Elminius modestus (d)
Elminius plicatus (ld)
Ralfsia verrucosa (ld)
Volsella neozelanicus (a)
Sypharochiton pellis-serpentis (f)
Lepsiella scobina (f)
Cellana radians (f)
Cellana ornata (o)
Urospora penicillaeformis (l) (autumn)

This association, which is included by Oliver (1923) in his "Shelled Animals Formation," has the widest range of distribution of any inter-tidal community in the region and is subject to the greatest variety of changes in environmental conditions.

a. **Chamaesipho Consociation**

Chamaesipho columna, the smallest of the common inter-tidal barnacles, is usually to be found forming a greyish-white, horizontal belt about the mark of M.H.W.N. At this tide level the community is a closed one in places of optimum development, but towards its upper limit (M.H.W.M.) the individual barnacles are more scattered, and species from higher associations, e.g., *Volsella neozelanicus,* may become locally dominant.

b. **Elminius—Scytothamnus Fasciation**

Elminius plicatus, the largest of the inter-tidal barnacles in this locality, is locally dominant just above M.S.L., where it may form a closed community, usually not exceeding 1 foot in vertical extent. *Chamaesipho columna* and sometimes *Caulacanthus spinellus* are common epiphytes on *E. plicatus.* The dark brown fronds of *Scytothamnus australis* are the prevailing feature of portions of the community, co-dominating with either *E. plicatus* or *E. modestus,* the latter mainly at lower levels just above the coralline turf. During periods of emergence the exposed parts of the thalli become dry and parched, while portions lying directly upon the barnacles are still quite damp.

c. **Elminius modestus Consociation**

This community may be present at any level between M.S.L. and M.L.W.N. Perhaps the most striking ecological attribute of *E. modestus* is its ability to exist in muddy water. At Narrow Neck it flourishes on the gently sloping dip face of the main reef above *Corallina,* where at times there is a layer of fine silt and mud ½ inch thick. *E. modestus* is equally at home on flat, vertical, or sloping faces, whether shaded or exposed to sun, and on both upper and under sides of boulders. Once established, it can withstand relatively strong tidal currents and wave action. It is prevented from colonizing all the available rock surface within its vertical range by competition, within narrower limits, from other animal communities, in particular those formed by the common rock oyster, *Saxostrea glomerata,* and by tubicolous polychaetes like *Hermella spinulosa* and *Vermilia carinifera.*

Chamaesipho and *E. modestus* owe their ubiquitous nature to their ability to reproduce in large numbers throughout the year (Moore, 1943) and to their wide tolerance with respect to their substrates.

d. **Saxostrea Consociation** (Fig. 9)

Vertical range: 6.5–3.5 feet. Between M.S.L. and M.L.W.N.

Exposure: 53–20 per cent.

Saxostrea glomerata occurs in a conspicuous belt, both upper and lower boundaries of which are sharply delimited. A species most consistent with regard to vertical range, *Saxostrea* shows relatively little variation in pattern of distribution in response to factors such as wave action, light incidence, and angle of slope of the substrate (Doty, 1946). The consociation usually gives way above and below to a balanoid community. On the main reef, however, which is nowhere higher than 6 feet, the oyster forms the uppermost belt.

The few associated species are nearly all animals. The gastropod *Lepsiella scobina* causes much damage by boring holes with its radula through the shell of the oyster, which it extracts in pieces. Powell (1947) records that *Lepsiella* can pierce an oyster shell in 45 minutes.

4. **Hermella—Vermilia Association**

Vertical range: 5.5–2.8 feet. From just below M.S.L. to just above M.L.W.M.

Exposure: 42–10 per cent.

Hermella spinulosa (d)
Chamaesipho columna (a)
Codium adhaerens (f)
Gelidium caulacantheum (o)
Vermilia carinifera (d)
Elminius modestus (a)
Centroceras clavulatum (o)

FIG. 9. *Saxostrea glomerata* consociation on a heavily eroded ledge near St. Leonard's Point.

Lunella smaragda (f)
Neothais haustrum (o)

An association dominated by the tubicolous polychaetes *Hermella spinulosa* and *Vermilia carinifera* is characteristic of the shaded (strike) faces of ledges on Narrow Neck Beach which are adjacent to sand. *Vermilia* nearly always occurs above *Hermella,* although the two species occasionally intermix. *Hermella* appears to be more tolerant of mud. At St. Leonard's Point it reaches maximum development, forming sandy hummocks which are easily eroded by wave action and which provide a place of refuge for numerous small crabs. *Vermilia carinifera* consists of calcareous tubes attached lengthwise to the substrate. The animal occupies only the opening of the tube and protrudes when lying in a small pool, but if the shell is exposed to air it retreats within the tube, which it closes with a shelly operculum.

Subordinate species include *Codium adhaerens,* forming compact, radiating cushions on either sandy or calcareous worm tubes (Fig. 10), together with the usual barnacles and molluscs, including chitons, limpets, *Lunella smaragda,* and occasionally *Neothais haustrum.*

Lower Mixed Algal Formation

5. Corallina—Hormosira Association (Fig. 11)

Vertical range: 3.7–0.8 feet. Between E.(H).L.W.N. and M.—E. L.W.S.

Exposure: 22.2–0.5 per cent.

Corallina officinalis (d)
Colpomenia sinuosa (a)
Codium adhaerens (f)
Caulacanthus spinellus (f)
Laurencia botrychioides (f) (summer)
Laurencia thyrsifera (o)
Dictyota ocellata (o)
Derbesia novae-zelandiae (r)
Polysiphonia sp. (r)
Chamaesipho columna (f)
Tethya fissurata (f)
Hormosira banksii f. *gracilis* (d)
Leathesia difformis (a)
Gelidium caulacantheum (f)
Enteromorpha procera f. *novae-zelandiae* (f)
Splachnidium rugosum (f) (summer)
Microdictyon mutabilis (o)
Symphyocladia marchantioides (o)
Dasya subtilis (r)
Lophurella caespitosa (r)
Elminius modestus (f)
Lunella smaragda (f)

Below the level of low water neap tides, there is an abrupt change in type of community: animals become of secondary ecological importance, and algae of one kind or another are physiognomic. There is also a notable increase in the number of species and, in general, a decrease in numbers of individuals. In the relatively sheltered waters of the Hauraki Gulf the *Corallina—Hormosira* association is the most widely distributed algal community in the inter-tidal region. Dull reddish-brown in gross appearance, it covers all the available space on flat or gently inclined rocks between low water neap and low water spring tide levels. Although *Hormosira banksii* often dominates a separate consociation in other localities (e.g., on Takapuna Reef), at Narrow Neck it is seldom found growing apart from *Corallina.* The regular line delimiting *C. officinalis* from the balanoid association above (Fig. 11) is broken here and there by upward penetration of the *Corallina—Hormosira* association along cracks in the rock which serve as drainage channels.

Hormosira seems unable to establish itself in large numbers on vertical or steep slopes. Towards the lower limit of the association it gradually drops out, and *Corallina* assumes dominance. The latter forms a short turf of tufted plants, apparently comparable to the algal turf described by Stephenson (1939, 1944) for South Africa.

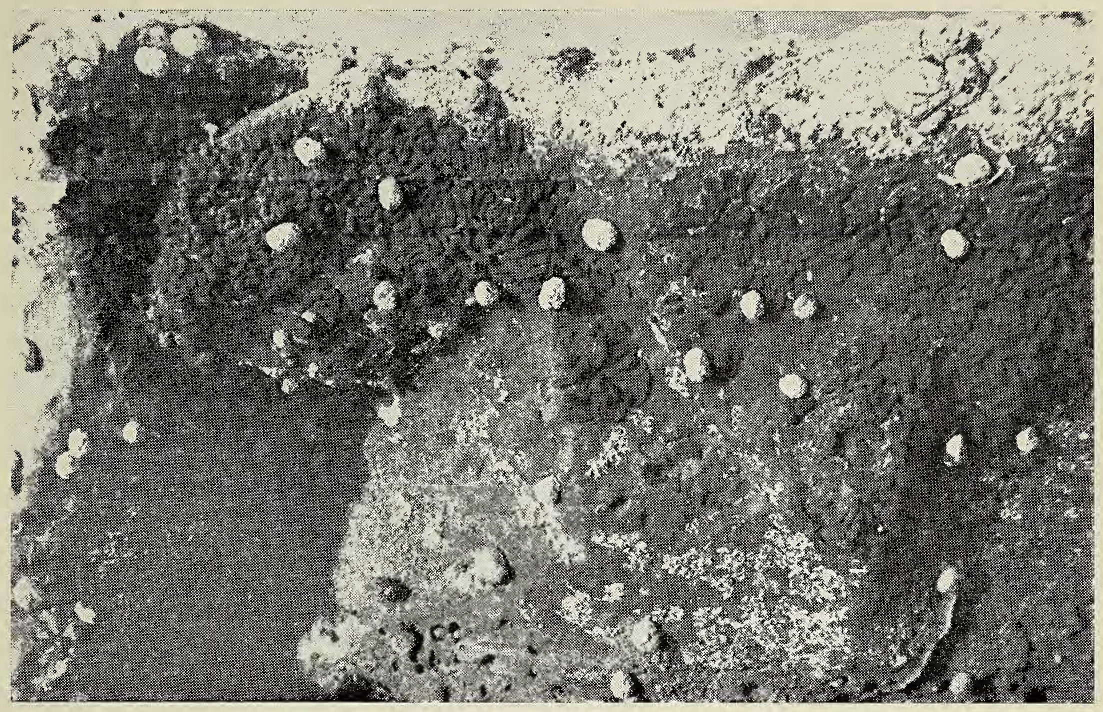

FIG. 10. *Codium adhaerens* growing above its usual level on a shaded, vertical rock face. *Chamaesipho columna* forms a white band above, *Lunella smaragda* is browsing on *Codium,* and *Vermilia carinifera* is scattered below.

FIG. 11. *Corallina—Hormosira* and balanoid associations on Crab Island, showing the abrupt cessation of the former with a slight increase in the level of the rock.

Nearly all of the subordinate algal species are epiphytic, chiefly because of the almost continuous covering of the substrate by the coralline turf, and most of them vary seasonally in abundance.

Caulerpa Clan

Within the limits of the above association, *Caulerpa sedoides* grows in isolated, cushion-like clumps between M.L.W.N. and M.L.W.S. The plant mass is so compact that other species are generally excluded, and hence the community is given the rank of clan (see p. 356).

6. **Encrusting Coralline Association**

Vertical range: 1.7–0.2 feet. Between M.L.W.S. and 0.4 feet below E.L.W.S.

Exposure: 3–0.2 per cent.

Corallina officinalis (basal portion) (d)
Peysonelia atropurpurea (f)
Laurencia thyrsifera (o)
Elminius modestus (o)
Melobesia sp. (d)
Acrosorium decumbens (o)
Chamaesipho columna (o)

On most steep rock faces which descend below low water mark, a pink band of encrusting algae separates the *Corallina—Hormosira* association from that dominated by species of *Carpophyllum* and *Ecklonia.* The most prevalent alga here is the basal, encrusting portion of *Corallina officinalis.* Growing with it are round or oval crusts of a species of *Melobesia,* which will readily colonize other surfaces besides rock, including shells of molluscs, and even smooth pieces of glass. Intermixed with these species is a darker red, hard crust with a slimy exterior, which appears to be *Peysonelia atropurpurea.* In shaded crevices, the delicate fronds of *Acrosorium decumbens* are sometimes to be found.

Carpophyllum and *Ecklonia* have their average upper limit (0.4 feet) in the Encrusting Coralline association. When growing at this level, holdfasts and stipes of the large brown algae may be exposed during a low spring tide, but the fronds usually escape desiccation by trailing in the water below.

7. **Mytilus—Attached Algae Community**

Vertical range: 0.7–0.2 feet. From E.L.W.S. to 0.4 feet below that level.

Exposure: 0.5–0.0 per cent.

Mytilus canaliculus (d)
Caulacanthus spinellus (ld)
Elminius modestus (a)
Corallina officinalis (d)
Ulva lactuca (l)

This community, which is of doubtful ecological status, is present locally where wave action is greater than usual for such a sheltered locality. It occurs at the extreme seaward end of St. Leonard's Point, both on the concrete sewer and on the rock ledges adjacent. During periods of exposure by the tide it is kept moist by surge from the constant swell or by spray if the wind is onshore. Under optimum conditions the principal dominant, *Mytilus canaliculus,* constitutes a closed community in which other members are forced to live as epiphytes on its shells. *Elminius modestus* is enabled to widen its vertical distribution in the inter-tidal region by colonizing the mussel shells.

Mytilus dominates in one other area—on a group of rocks outcropping from the submarine continuation of Narrow Neck Reef about 500 yards from the shore and 300 yards from the end of the Main Reef. Even on a calm day there is a considerable swell round these rocks. Associated with *Mytilus* here are dense clumps of *Ulva lactuca,* which does not occur on the Main Reef.

Sublittoral Brown Kelp Formation

8. **Carpophyllum—Ecklonia Association**

Vertical range: 0.4 feet–. From E.L.W.S. to below the reach of all tides.

Exposure: 0.3–0.0 per cent.

Carpophyllum maschalocarpum (d)
Carpophyllum plumosum (d)
Ecklonia radiata (d)

Carpophyllum flexuosum (d)
Sargassum undulatum (f)
Sargassum sinclairii (f)
Cystophora torulosa (f)
Ectocarpus indicus (f) (summer)
Glossophora kunthii (la) (summer)
Pterocladia lucida (l)
Myriogramme gattyana (l)
Zonaria subarticulata (o)
Cystophora retroflexa (o)
Cladhymenia oblongifolia (o)
Acrosorium decumbens (o)
Schizymenia novae-zelandiae (r)
Grateloupia polymorpha (r)
Myriogramme oviformis (f) (summer)

The present account is intended to deal only with communities of the inter-tidal region; but since the dominant species in the sublittoral fringe (i.e., between 0.6 and 0.0 feet) include those of the *Carpophyllum*—*Ecklonia* association, it will be discussed here.

An association in the sublittoral region dominated by one or more species of *Carpophyllum* is characteristic of rocky districts of the east coast of New Zealand (Oliver, 1923). Narrow Neck is no exception. The only New Zealand species not present is *C. elongatum*, the chief ecological requirement of which is deep, transparent water (Cranwell and Moore, 1938). At Narrow Neck, *Carpophyllum* and *Ecklonia* are present almost everywhere within their bathymetric limits. *C. plumosum* dominates in shallower and more sheltered habitats, and is especially common on the protected western fringe of the Main Reef (Fig. 1). *C. maschalocarpum* is by far the most abundant of the three species of *Carpophyllum* in the locality. It extends almost continuously from the base of the tide pole on Crab Island, round the seaward face of the latter, and along both sides of the Main Reef (Fig. 1). In the shallower channel between reef and shore *C. plumosum* and *Ecklonia radiata* are more physiognomic. The latter is equally abundant on both eastern and western fringes of the reef. In general, *C. flexuosum* is more typical of deeper water than *C. maschalocarpum* and *C. plumosum*, though all three flourish about A.H.B. Datum.

The upper limit of the association is remarkably constant. There appears to be a gradation in length of thallus which increases with depth at which the holdfasts are attached. This may be a response of the individual plants in connection with the optimum depth of water for photosynthesis.

A heavy epiphytic flora and fauna is supported by mature thalli of the large brown algae, and is composed mainly of diatoms, hydroids, and delicate red algae such as *Myriogramme oviformis* and *Acrosorium decumbens.* The abundance of diatoms is enhanced by the relatively slack tidal currents and the prevailing turbidity of the water.

Seasonal Communities

Porphyra umbilicalis and *Bangia vermicularis* form a winter aspect society on exposed ledges between M.H.W.N. and M.H. W.S. *Bangia* usually persists until summer.

About the level of M.L.W.N., spring and summer communities of *Myriogloia lindauerii* and *Helminthocladia australis* may be found. Both species are influenced adversely by sand.

Towards the lower limit of the balanoid association, *Splachnidium rugosum* grows in dense or isolated patches in late summer and autumn, dying away with the onset of winter.

Seasonal species do not, as a rule, reappear the following year in exactly the same situation as in the previous one.

Several points which require further commentary arise out of this discussion of the different associations:

1. The upper and lower limits given in feet represent the average for each association concerned, and do not imply that the dominant species cannot live at other levels. For instance, the lower limit of the balanoid association is 3.6

feet, but both *Chamaesipho columna* and *Elminius modestus* occur in the Encrusting Coralline association, 2 feet below.

2. Cranwell and Moore (1938) list *Lichina pygmaea* and *Melaraphe oliveri* as the chief dominants in the "supralittoral" or "splash zone" at Narrow Neck. However, *Lichina* does not exist as a dominant here, and it has been shown from the leveling survey that *Melaraphe* does not normally occur above E.H.W.S.
3. The same association-complex is to be found with only slight local modifications farther north on Takapuna and Milford Reefs where the substrate is volcanic basalt.

CRITICAL LEVELS

Inasmuch as the inter-tidal region may be divided into a number of zones, each characterized by certain species which are absent or insignificant in other zones, it may be assumed that some levels are more important than others in restricting the upward or downward extension of a species. Colman (1933), David (1943), Chapman (1943), and Evans (1947) have investigated the problem of critical levels[5] in Great Britain, and Doty (1946) has made similar studies on the Pacific coast of North America. The fact that David found only one such level at Aberystwyth identical with one of Colman's levels at Wembury Bay, namely E.(L).H.W.N., indicates that each locality should be treated on its own merits. Both the number and the position of critical levels appear to vary from coast to coast.

From an examination of Figure 7, it is apparent that there are certain relationships between the total number of species, the number of upper and lower limits, and the level on the shore. For example, six species have their lower limits and eight species have their upper limits of vertical distribution between the levels of 9 and 12 feet, making a total of 14 limits, while only nine species occur *between* those levels. Between 5 and 8 feet, on the other hand, there is a total of eight limits, with the occurrence of nine species. The concept of critical levels is based on the assumption that the fewer the number of species and the greater the number of upper and lower limits at a certain level, the more critical it will be in limiting the vertical range of a species or community.

The relationship between height on the shore, number of species, and number of upper and lower limits of species was investigated from data obtained in the leveling survey. Colman's (1933) method for finding critical levels was followed. By taking from Figure 7 the number of species with limits between −1 and +2 feet, 0 and +3 feet, +1 and +4 feet, and so on, three curves were constructed (Table 2 and Fig. 12).

TABLE 2
RELATIONSHIP OF HEIGHT ON SHORE AND SPECIES

FEET ABOVE OR BELOW A.H.B.D.	LOWER LIMITS	UPPER LIMITS	TOTAL LIMITS	TOTAL SPECIES	DIFFERENCE BETWEEN TOTAL SPECIES AND TOTAL LIMITS
+12 – +15	0	1	1	1	0
11 – 14	0	3	3	3	0
10 – 13	1	9	10	9	1
9 – 12	6	8	14	9	5
8 – 11	6	7	13	10	3
7 – 10	7	3	10	10	0
6 – 9	5	4	9	9	0
5 – 8	3	5	8	9	-1
4 – 7	4	3	7	8	1
3 – 6	6	8	14	12	2
2 – 5	10	7	17	13	4
+1 – +4	11	8	19	13	6
0 – +3	9	4	13	8	5
−1 – +2	5	3	8	6	2

In Figure 12, curve A represents the number of lower limits at each level, curve B the

[5] A critical level may be defined as a level at which a relatively great number of species reach the upper or lower limit of their vertical ranges.

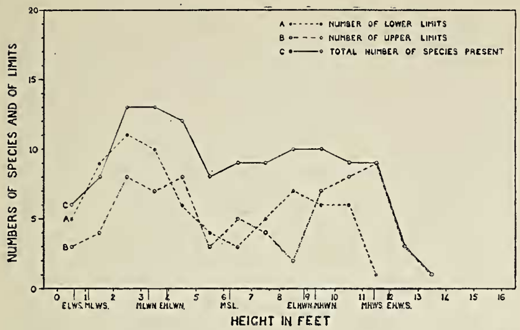

FIG. 12. Graph indicating the relationships between the number of species, and of upper and lower limits at different heights on the shore.

number of upper limits, and curve C the total number of species. There are two maxima in both A and B, one low down on the shore, and one higher up. The greatest number of both upper and lower limits occurs between +1 and +4 feet, i.e., between M.L.W.N. and M.L.W.S. (= M.L.W.M.). Curve A (lower limits) has a second pronounced maximum between 7 and 10 feet, just below E.(L).H.W.N. Curve B (upper limits) rises to a peak between 10 and 13 feet, i.e., at M.H.W.S. There is a secondary maximum at E.(H).L.W.N.

In all cases but one (between 5 and 8 feet), the total number of species is *less* than the total number of limits at any one level. At both Wembury and Cardigan Bays, however, the total number of species at each level always exceeded the total number of limits: that is, inter-tidal species in these localities have, in general, a wider vertical range than those at Narrow Neck. This difference may prove to be correlated with lower average minimum temperatures in Great Britain, associated with higher latitudes.

A further graph was constructed by plotting total limits minus total number of species against height on the shore (Fig. 13). Again there were two maxima—at M.L.W.M. and M.H.W.M.—with a subsidiary maximum between M.L.W.S. and E.L.W.S.

It is possible that these levels may be of critical significance in determining vertical

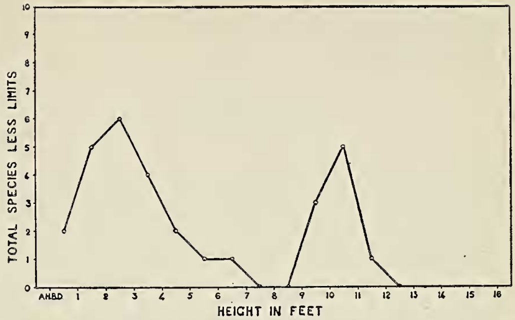

FIG. 13. Graph obtained by plotting the number of species minus the number of limits against height on the shore. The two peaks indicate the positions of two critical levels (M.L.W.M. and M.H.W.M.). M.–E.L.W.S. (between 1 and 2 feet) may also be critical.

zonation at Narrow Neck. Presumably, immediately above or below each critical level, there is a change in one or several of the factors comprising the external environment. This change must be of sufficient magnitude to restrict or inhibit optimum growth of the individuals concerned and involves a consideration of the nature of factors operating in the inter-tidal region. Investigations on the ecological factors are being continued, and it is hoped that further results will be published at a later date.

SUMMARY

An account is given of the plant and animal communities at Narrow Neck Reef, Auckland, in relation to their levels on the shore and to the range of exposure annually undergone by each. Four leveling traverses were made in different parts of the area to illustrate the main patterns of zonation.

The problem of critical levels is discussed. The following levels may be regarded as critical in determining zonation at Narrow Neck:

	TIDE LEVEL	NUMBER OF SPECIES	NUMBER OF LIMITS	EXPOSURE *per cent*
I.	M.L.W.S.–E.L.W.S.	8	13	1
II.	M.L.W.M.	12	19	6
III.	M.H.W.M.	9	14	92

The least critical level is 8.0 feet, nearly 1 foot below E.(L).H.W.N.

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